1959

Developmental vegetative morphology of Avena sativa

Gilford John Ikenberry Jr.
Iowa State University

DEVELOPMENTAL VEGETATIVE MORPHOLOGY OF *AVENA SATIVA*

by

Gilford John Ikenberry, Jr.

A Dissertation Submitted to the
Graduate Faculty in Partial Fulfillment of
The Requirements for the Degree of
DOCTOR OF PHILOSOPHY

Major Subject: Plant Morphology

Approved:

Signature was redacted for privacy.
In Charge of Major Work

Signature was redacted for privacy.
Head of Major Department

Signature was redacted for privacy.
Dean of Graduate College

Iowa State University
Of Science and Technology
Ames, Iowa

1959

TABLE OF CONTENTS

INTRODUCTION

Avena sativa L. has been the subject of numerous investigations, in particular genetic, physiological, and pathological studies. The objective of many studies has been to increase the yield or improve the quality of the crop. Basic studies have been directed toward the interpretation of results of applied research. Our knowledge of the oat plant still remains incomplete in many areas, particularly some aspects of the development of the plant.

The present investigation was undertaken to provide more complete information on the structure and development of the post-dormant vegetative phase, to the initiation of the flowering phase. Special attention is given to resumption of growth in the dormant embryo, initiation and development of leaves and buds, vascular ontogeny, and structure of the internodes.

REVIEW OF PERTINENT LITERATURE

The structure of the dormant embryo of Avena has been described by Avery (5), who compared the structure and course of differentiation of the procambium in the seedling axis with that of maize and wheat. The early vascular pattern of the shoot and the development of the first internode (mesocotyl) have been described in Avena by Boyd and Avery (8). Avery and Burkholder (6) investigated the structure and growth of the Avena coleoptile, and reported that cell division ceases by the time the coleoptile is one-fourth its mature length and that cell elongation is greater in the basal region. Holt (21) described some features of the normal developmental histology of the oat seedling in relation to the response of plants treated with 2,4-dichlorphenoxyacetic acid. The normal seedling was found to have four leaf primordia at emergence from the soil.

Yung (37) described the embryo, early seedling and foliage leaf development in the rice plant and reported a close resemblence to Avena. The mature rice embryo was reported to have no lateral seminal roots. The developmental anatomy of the wheat seedling has been studied by McCall (24). He described the divergence of the scutellar trace from the axis as the second node, the third node being the node of the coleoptile. The first internode in maize was described by

Tucker (35) to be, histologically, a transition zone. Toole (34) described the morphological changes occurring during germination of the maize caryopsis and demonstrated that mitotic reactivation is initiated in the radicle after 24 hours. More recently, Picklum (26) studied histological and cytological changes which occur during germination of the maize caryopsis and recorded the relative time of mitotic reactivation for the various organs of the embryo.

The interpretations of the homologies in the embryo have been adequately reviewed by Avery (5), McCall (24), and Boyd and Avery (8). The more recent work by Boyd and Avery (8), Reeder (27), and Tucker (35), strengthens the interpretations by Avery (5) in which he states that: 1) the coleoptile is the first leaf above the single cotyledon, 2) the first internode (mesocotyl) extends from the cotyledonary node to the coleoptilar node, and 3) the epiblast is probably of little morphological significance.

Reviews of earlier studies on the shoot apex have been adequately presented by Foster (13). Foster (13, 14) and Gifford (17) have reviewed the comparative and developmental morphology of the shoot apex in seed plants. General descriptions and reviews of the developmental morphology of the grasses with particular emphasis on the shoot apex have been presented by Barnard (7), Evans and Grover (12), and Sharman (30, 33).

Rösler (28) studied leaf and bud initiation in Triticum vulgare L. He suggested that a single common initial cell gives rise to the internal tissues of the apex. He found that hypodermal cells as well as dermotogen cells are involved in leaf initiation, but he was uncertain whether cells beneath this layer are involved.

Sharman (30, 32) has described the shoot apex in Agropyron repens (L.) Beauv. as having three thimble-shaped layers, designated as dermatogen, hypodermis, and subhypodermis, all of which enclose a central core. He found that leaf primordia can first be detected by periclinal divisions in the dermatogen, and that the young leaf is derived entirely from the dermatogen and hypodermis. He interpreted the dermatogen and hypodermis of axillary buds as being derived from the same layers of the main axis, while the subhypodermis and central core of the bud are derived from the subhypodermis of the main axis.

Abbe, et al. (1, 2, 3) found that the increase in size in the shoot apex of maize during successive plastochrons was due to an increase in cell number, the cell size remaining constant. They also found that the duration of successive plastochrons decreases markedly during the initiation of leaves 7 through 14.

Sharman (31) studied the developmental anatomy of the shoot of Zea Mays L. He found that periclinal divisions in

the dermatogen (protoderm) and underlying cells indicate the initiation of a leaf. He speculated that the marginal meristem of a leaf is concerned in the formation of the bud which will later appear in the axil of the leaf below.

Kliem (22) described the formation of leaf primordia in Avena sativa, designating everything inside the single tunica layer as the corpus, although he reported a hypodermis in older meristems. Predominantly anticlinal divisions were noted in the hypodermis whereas those in the sub-hypodermal region were largely periclinal. Kliem favored the concept that the corpus originates from one or two initials or groups of initials just beneath the tunica.

Hamilton (20) compared the developmental anatomy of the shoot in four varieties of Avena grown at 16°C. and 28°C. The "formative period" was found to extend over the first 3 weeks. She designated the regions in the apical meristem as dermatogen, hypodermis, subhypodermis, and core.

Esau (11) has reviewed the literature on the origin and development of primary vascular tissues in the seed plants.

The developmental anatomy of the vegetative organs in sugar cane has been studied by Artschwager (4). He stated that the vascular bundles in this species are of the closed, collateral monocot type, but variations occur at the nodes and in the lower leaf sheath.

The ontogeny of the vascular bundle in Zea mays has

been studied by Esau (10). It was found that the larger bundles of the leaf arise from larger procambium strands. The procambium strand increases in size by predominantly tangential longitudinal divisions. The protophloem matures before the protoxylem, and both of these are destroyed during the maturing of the metaphloem and metaxylem. Esau interprets the protophloem and protoxylem as the conducting tissues of the elongating shoot, whereas maturation of the metaxylem and metaphloem is delayed until the organs complete their elongation. The bundle sheath is derived from the procambium, but at maturity, the peripheral cells of the sheath are indistinct from the adjacent parenchyma or hypodermal sclerenchyma.

In a study of the ontogeny of the first internode (mesocotyl), Tucker (35) found the sequence of vascular tissue differentiation is: protophloem, protoxylem, metaphloem, and metaxylem. She found that the procambium, protophloem, metaphloem, and metaxylen differentiate in a continuous acropetal pattern; while the protoxylem differentiates from the coleoptile node downward in a discontinuous manner.

Cheadle (9) investigated the occurrence and structure of vessels in the Monocotyledoneae. He determined that all the metaxylem tracheary elements in the stem and leaf in grasses should be interpreted as vessels with perforation plates.

Hamilton (20) observed that differentiation of the xylem is more precocious and occurs at a higher level in the procambium strands of oat plants grown at 28°C. than those grown at 16°C.

The effect of dark and light on the xylary elements of the first internode in Avena was studied by Goodwin (18). He observed the successive differentiation of annular, spiral, and pitted elements, and emphasized the presence of intermediate types. He found that differentiation in the first internode is largely acropetal. He discussed the close correlation between the inhibition of elongation in the first internode by light and the formation of pitted xylary elements.

In studies on lodging in cereal grasses, Welton and Morris (36) determined that the zone of hypodermal sclerenchyma of the internode is wider and its cell walls thicker in lodging resistant oat varieties. Certain oat culm characters and their relationships to lodging were discussed by Hamilton (19). He concluded that a possible index to lodging could most reliably be based on: 1) height of plant, together with the diameter of the second internode above the ground, 2) size and number of vascular bundles, 3) percentage of lignin. Norden (25) reviewed the literature on lodging resistance in oats, in conjunction with his genetical studies of factors associated with lodging resistance.

MATERIALS AND METHODS

Three agronomic varieties of Avena sativa were used for this study. The varieties Cherokee and Clintland were used in studies involving germination under controlled conditions, whereas the varieties Clintland and Marion were used for field collections.

Plant material for the study of imbibition, reactivation, and growth prior to emergence from the soil was grown at a constant temperature of 20°C. in the germinators of the Seed Laboratory, Iowa State University. Caryopses were planted in plastic light-tight refrigerator crispers which contained 3 inches of Vermiculite. Collections were made at 3 to 6 hour intervals.

Plantings for field material were made on April 15, 1957, at the Iowa State University Agronomy Farm. Seedlings emerged from the soil on April 23. Two adjacent 100 foot "drill-strips" were planted at the rate of 3 bushels per acre. One strip was seeded to the variety Marion, a weak-strawed variety, and the other strip was seeded to the variety Clintland, a lodging resistant type. Collections were made on alternate days throughout the growing season.

Stages up to emergence from the soil were obtained from the germinator, whereas later stages were obtained from the field. Therefore, the designation "days after planting" is

the sum of days required for emergence at 20°C. plus the days after emergence in the field.

Plants were fixed in Craf III and processed for sectioning in paraffin. A dioxan-tertiary butyl alcohol or a modified ethyl alcohol-tertiary butyl alcohol series was used in dehydration. Sections were cut from 8 to 14 microns in thickness. Slides for photomicrography were pre-stained lightly in hemalum before being stained in safranin-fast green.

For the study of cell types, individual vascular bundles were dissected from previously fixed plant parts and treated by Jeffrey's Method for 4 hours (18). Bundles were then mounted in 70% lactic acid. A moderate pressure applied to the cover slip served to separate the vascular elements while maintaining their positional relationships. Camera lucida drawings were made using a phase contrast microscope. Positional relationships and structural features deduced by maceration were confirmed by serial paraffin sections.

OBSERVATIONS AND RESULTS

The Dormant Embryo

The dormant oat embryo lies near the base of the caryopsis with the anterior side of the embryo adjacent to the aleurone and pericarp, and its posterior surface contiguous with the endosperm. The central and upper portion of the embryo axis is partially encased by the scutellum. The extension of the scutellum just above the coleoptile is the so-called ventral scale. The developing axis is greatly exceeded in length by the distal portion of the scutellum which has a darkly staining epithelial layer in contact with the endosperm. The coleoptile has a small slit-like opening in the anterior side.

A minute bud primordium is located in the axil of the coleoptile. The short, rounded dome of the shoot apex is subtended by two foliage leaf primordia. In cross-section, the first leaf completely encircles the apical meristem whereas the second leaf is a small crescent.

The coleorhiza encloses, and is contiguous with a well developed radicle and root cap. The epiblast is a flattened structure that extends upward from the anterior surface of the coleorhiza. There are two, rarely three, endogenous seminal roots extending laterally and downward from the level of the scutellar node.

Vascularization in the dormant embryo is represented by

partially differentiated procambium strands. The scutellar node (scutellar plate) is a zone of anastomosing procambium immediately proximal to the immature stele of the radicle. In addition to the procambium extending from this point into the seminal roots, two main procambium strands extend toward the plumule. The larger posterior strand bends sharply near the region of the coleoptile node, where it receives two strands from the coleoptile, then continues toward the tip of the scutellum where it branches into numerous reflexing strands (Fig. 1). The anterior strand extends to a level slightly above the coleoptile node, at which point it becomes continuous with the mid-procambium strand of the first leaf.

In transverse section, the large central procambium strand of the scutellum has, in the more proximal half, one or two annular or spiral protoxylem elements adaxially, and two to five protophloem elements abaxially (Fig. 2). The first foliage leaf of the dormant embryo has 11 to 13 procambium strands which vary in size and stage of development. The large strand of the mid-rib has two to three protophloem elements and one differentiated protoxylem vessel. One protophloem element is evident in each of the two vascular strands which are located mid-way between the mid-vein and lateral edges of the first leaf. The coleoptile has one to two protophloem elements in the basal region of each of the two lateral provascular strands, but no protoxylem is evident in

Fig. 1. Cross-section through the distal portion of the scutellum in a dormant embryo. Note the numerous reflexing procambium strands which branch from the main procambium strand. (X 100)

Fig. 2. Cross-section of the procambium strand in the scutellum of the dormant embryo. The section is at the level of the stem apex. (X 200)

Scutellum	(S)
Endosperm	(ES)
Epithelial layer	(EP)
Protophloem	(PP)
Protoxylem	(PX)
Coleoptile	(CT)


ES
EP
1
ES
2

this structure.

The first internode (mesocotyl) has one to three protoxylem and protophloem elements in each of the two main procambium strands, the anterior strand being larger and more highly differentiated. The stele of the radicle has seven or eight protophloem sieve tubes arranged circumferentially around a central, thin walled, immature metaxylem element. Protoxylem is not evident although areas of its future development are distinguishable.

Resumption of Growth

Imbibition and initial cell enlargement

The first indication of growth and reactivation in the Avena embryo may be detected less than 12 hours after the beginning of imbibition. Enlargement of cells occurs in the coleorhiza and epiblast, as well as less pronounced cell enlargement in the region of the scutellar node and unexpanded mesocotyl. The coleorhiza and radicle rupture the pericarp before 12 hours as a result of this enlargement. The cells of the root cap, radicle, and coleorhiza are contiguous at this stage (Fig. 3).

Subsequently, the radicle begins to elongate. More rapid longitudinal expansion of the coleorhiza causes it to separate from the root cap (Fig. 4). The radicle has penetrated the lemma and palea by 24 hours. Continued enlargement in the

Figs. 3-6. Projection drawings of the early stages of post-dormant growth in the Avena embryo axis. Small "x"s indicate the areas of mitotic activity. (X 25)

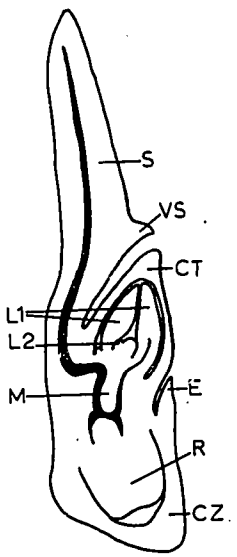
Fig. 3. The dormant embryo.

Fig. 4. The embryo 24 hours after imbibition has begun. Mitosis was first evident at this stage.

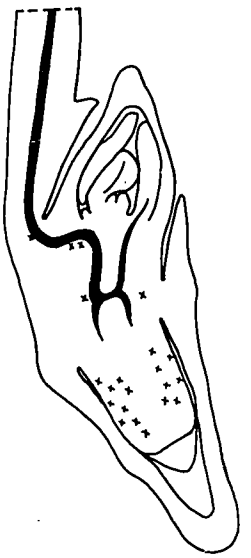
Fig. 5. The embryo axis 27 hours after imbibition has begun.

Fig. 6. The embryo axis 36 hours after imbibition has begun. Mitotic reactivation has occurred in all organs of the axis by this time.

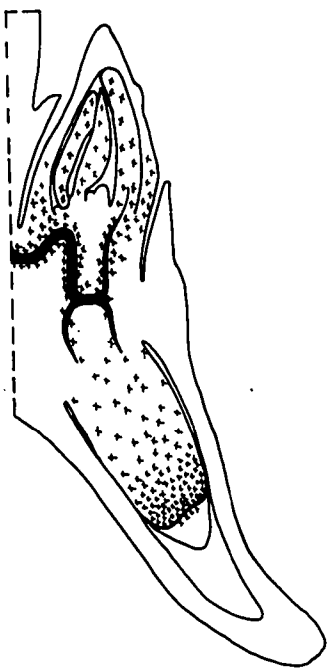
Scutellum	(S)
Ventral scale	(VS)
Coleoptile	(CT)
First foliage leaf	(L1)
Second foliage leaf	(L2)
Epiblast	(E)
First internode	(M)
Radicle	(R)
Coleorhiza	(CZ)



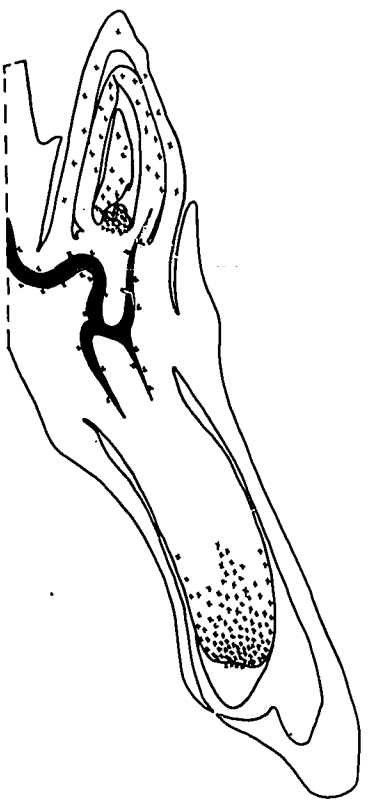
3



4



5



6

coleorhiza causes complete separation from the primary root by 27 hours (Fig. 5).

Continued growth of the coleorhiza, epiblast, and scutellum is by cell enlargement only, since mitotic divisions have not been observed in these structures during germination. Fig. 6 indicates the regions of relatively greater cell enlargement at 36 hours. At this stage the radicle has penetrated the coleorhiza. Distinct regions of cell division and cell enlargement which are found in the mature root have been established in the radicle at this time.

By 60 hours the epithelial cells of the expanding scutellum have undergone extensive radial elongation. Epidermal cells of the epiblast have given rise to numerous multicellular hairs at this stage.

Mitotic reactivation

Mitotic activity was found to occur by 24 hours after the dry kernels were placed in moist vermiculite in the germinator at a constant 20°C. The first mitotic divisions were observed in the epidermis (protoderm) and cortex (periblem) of the radicle, some distance above the root histogens (Fig. 4). From this region, mitosis is initiated progressively toward the root apex, including the stele, root histogens, and calyptrogen.

By 27 hours, mitotic figures are abundant in the radicle,

seminal roots, area of the coleoptile node, and first leaf. Some mitotic activity is also present in the basal portion of the coleoptile and in the region of the mesocotyl and vascular arch (Fig. 5). The procambial cells of the various organs are particularly active. Nuclei of the shoot apex and second leaf are not yet dividing.

Mitotic figures can be found in the second leaf primordium and near the base of the apical dome at 30 hours.

Complete mitotic reactivation has occurred by 36 hours. Mitotic divisions are most numerous in the stem and root apical meristems, the second leaf primordium, and in the developing vascular strands (Fig. 6). Division figures are present, although somewhat less frequent, in the first leaf, particularly at the margins and in the procambium strands; and in the coleoptile.

Initiation and Ontogeny of the Leaf

The shoot apex of the embryo in the dormant Avena caryopsis is a short dome, subtended by the primordia of two foliage leaves. Longitudinal sections of the stem tip at this stage indicate differentiation into an outer single layer of cells, the tunica, and an inner zone of cells, the corpus. Periclinal cell division in the tunica indicates the initiation of the next leaf primordium, the third foliage leaf. This division occurs a short distance below the stem

tip and may be detected in both transverse and longitudinal sections (Figs. 7, 8). Reference to foliage leaves by number in this study indicates their acropetal sequence of initiation.

From the zone of initiation, periclinal divisions spread laterally around the apex, accompanied by random divisions in the corpus, which together give rise to a crescent-shaped ridge that partially encircles the stem (Fig. 9). Further lateral spread of cell divisions results in the formation of a collar-like leaf base that completely surrounds the stem. This annular leaf primordium elongates by cell division in the meristematic margin, and the leaf soon arches over the apex. Successive loci of initiation occur directly opposite and above preceding ones, and thus initiate the two ranked, distichous, arrangement of leaves.

Leaf initiation soon involves both tunica and corpus, hence some of the inner tissues of a leaf are derived from the surface layer, the tunica or protoderm. Intercalary growth at the leaf base gives rise to the tubular sheath. The ligule is derived from the adaxial surface layer, protoderm, of the leaf primordium, by periclinal cell divisions. It is first detected on the third or fourth leaf from the stem tip at the level of the apex.

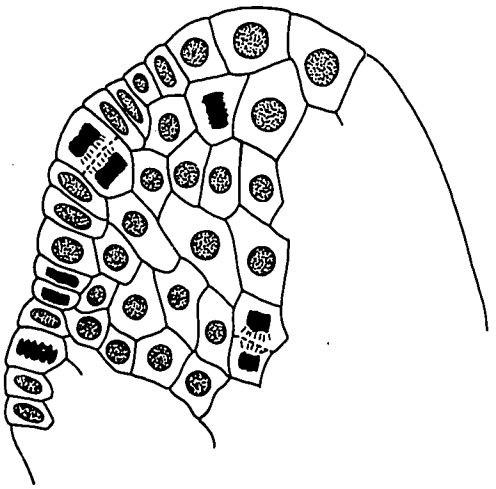
As the leaf primordium continues to expand, the meristematic lateral margins meet and then overlap. The edge of

Figs. 7-9. Projection drawings of the stem apex during the initiation of the fourth foliage leaf. (X 440)

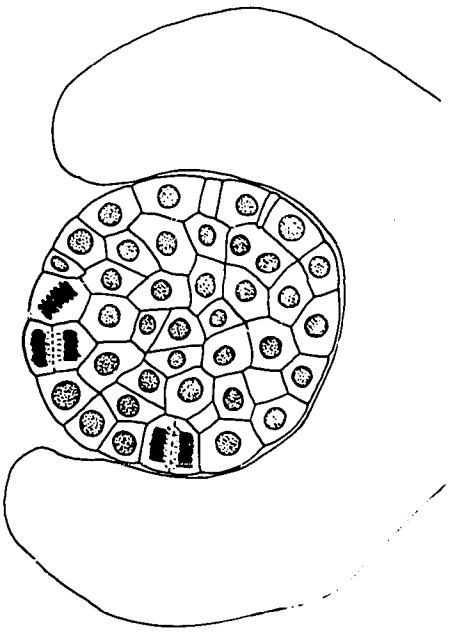
Fig. 7. Longitudinal section of the stem apex showing a periclinal division in the tunica. (45 hours after imbibition)

Fig. 8. Transverse section of the stem apex showing a periclinal division in the tunica. (45 hours after imbibition)

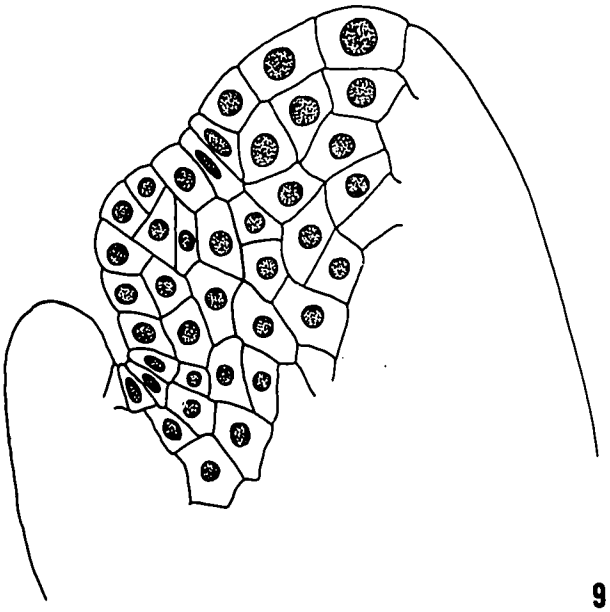
Fig. 9. Longitudinal section of the stem apex showing a small leaf primordium which arises as a result of both periclinal and anticlinal divisions in the tunica. (60 hours after imbibition)



7



8



9

a leaf consists of a single row of cells except in the distal region. The maximum thickness of the leaf in cell layers is attained approximately eight to 12 cells from the edge. Further increase in leaf thickness can be attributed largely to cell enlargement.

The main culms of the three varieties observed in this study invariably gave rise to nine foliage leaves. There are rarely more than five expanded leaves visible at any one time during the growing season, and only the last two or three are functional at maturity.

The third foliage leaf is initiated within 45 hours after the caryopsis has been placed under favorable conditions for germination. Initiation of the fourth leaf and morphological changes which occur in the shoot apex during the subsequent plastochron* are illustrated by the series of drawings in Figs. 10, 11, 12, 13, and 14.

Successive leaf primordia can be detected at intervals of 1 to 3 days prior to the formation of inflorescence primordia. There is a definite shortening of the plastochron as the axis approaches transition. This is associated with the gradual lengthening of the shoot apex during the initiation of the last three phytomers. Compare the vegetative apex in Fig. 15 with transitional apex in Fig. 16. Transition to the

---

*A plastochron is the time interval between the initiation of successive leaf primordia.

Figs. 10-14. Series of drawings showing the changes which occur in the shoot apex during a plastochron involving the initiation of the fourth foliage leaf. Leaves are numbered according to their sequence of initiation. (X 440)

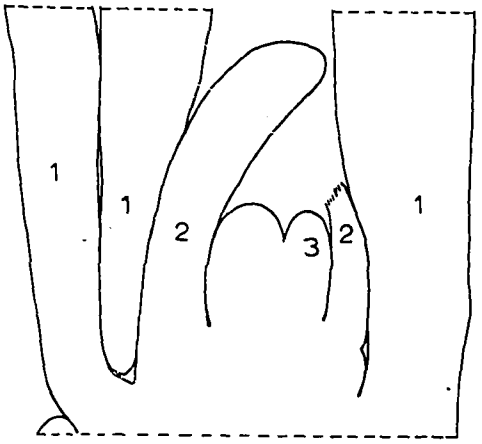
Fig. 10. Apex prior to initiation of fourth leaf. (84 hours after imbibition)

Fig. 11. Initiation of the fourth leaf. (120 hours after imbibition)

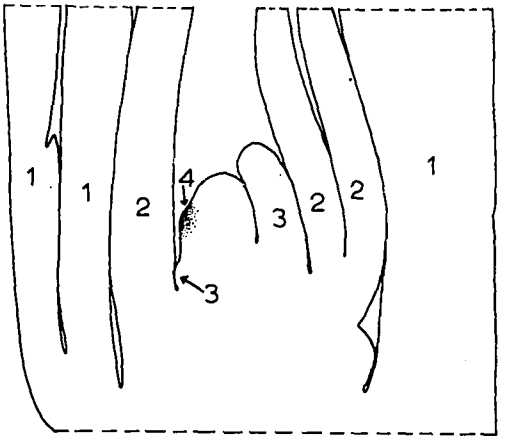
Fig. 12. Enlarging of the fourth leaf primordium. (126 hours after imbibition)

Fig. 13. Apex just prior to initiation of the fifth leaf. (144 hours after imbibition)

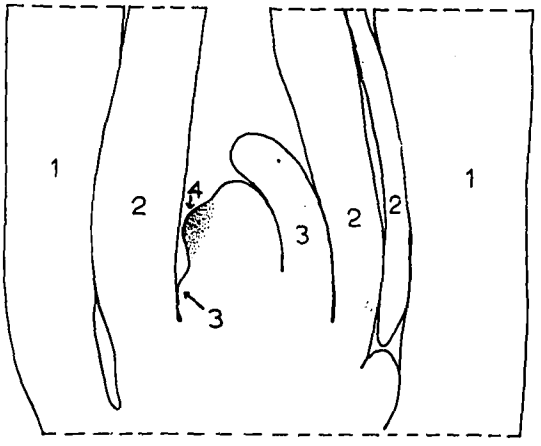
Fig. 14. Initiation of the fifth leaf. The fourth leaf has nearly encircled the shoot apex. (168 hours after imbibition)



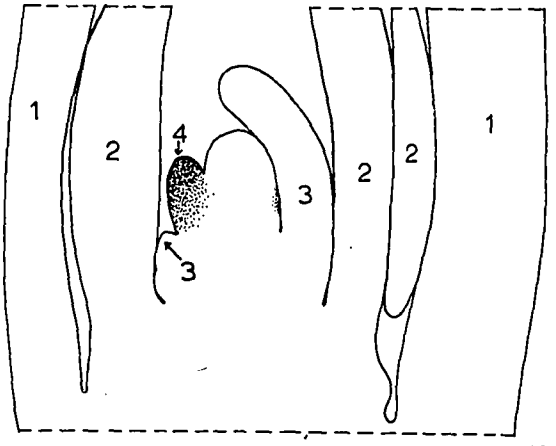
10



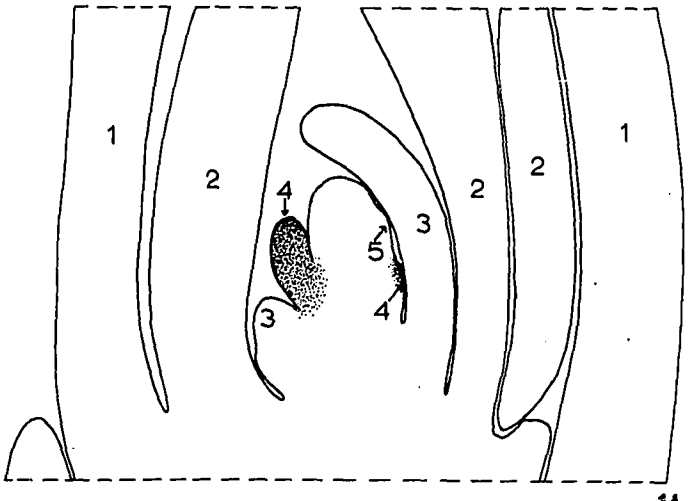
11



12



13



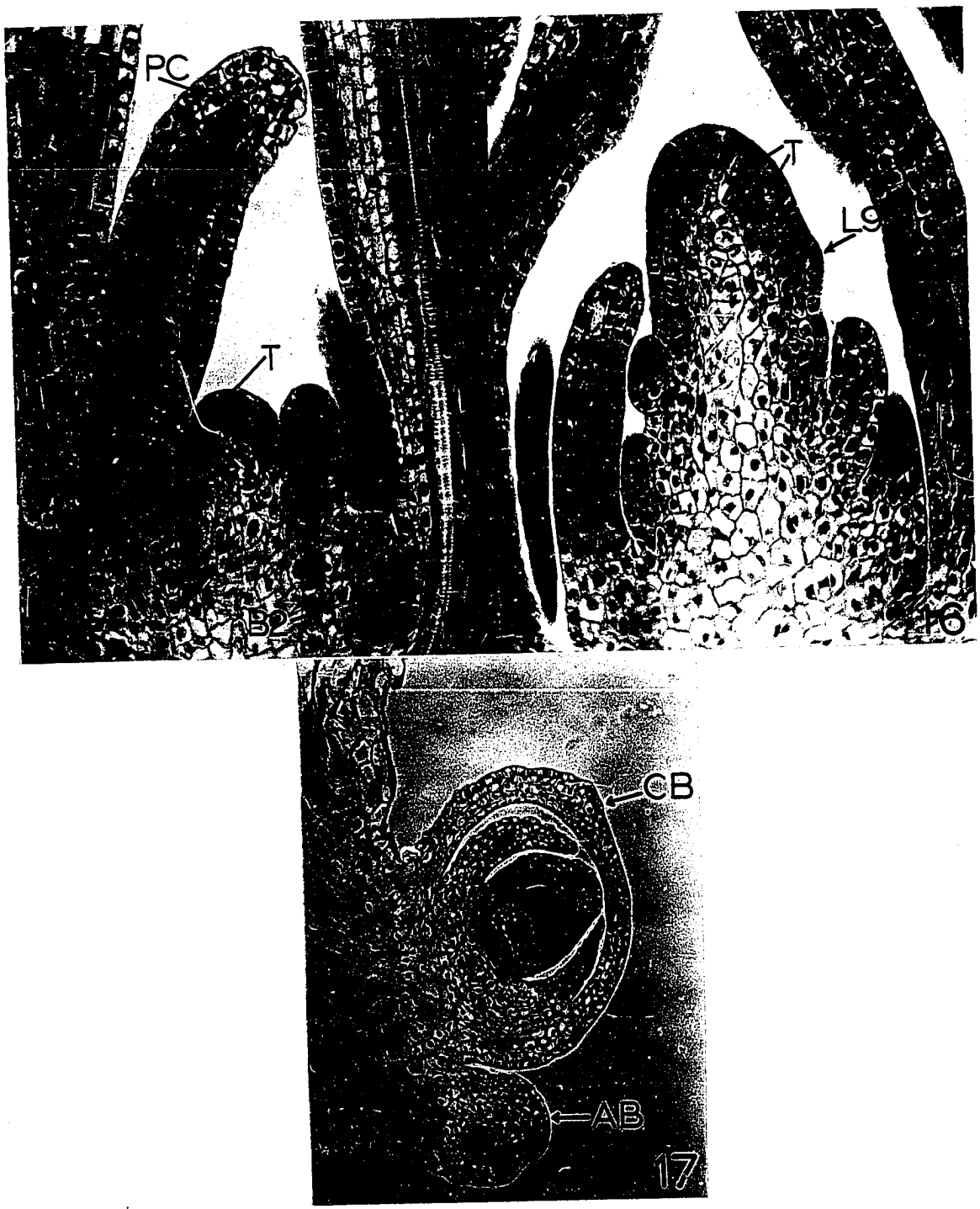
14

Fig. 15. Shoot apex at emergence from the soil. This stage is just prior to the initiation of the fifth leaf. (4 days after planting, X 200)

Fig. 16. Shoot apex at initiation of ninth foliage leaf. Note the indication of a two-layered tunica. (13 days after planting, X 200)

Fig. 17. Main bud and accessory bud in the axil of the coleoptile. (17 days after planting, X 100)

Procambium	(PC)
Second foliage leaf	(L2)
Third foliage leaf	(L3)
Ninth foliage leaf	(L9)
Corpus	(C)
Tunica	(T)
Main coleoptile bud	(CB)
Accessory coleoptile bud	(AB)


PC
T
BP
T
LP
16
CB
AB
17

flowering phase, and initiation of inflorescence branch primordia has occurred by 10 days after emergence. Table 1 indicates the time of initiation of the leaves and transition to the floral phase, and relates this to the external appearance of the plant.

Initiation of the Axillary Bud and Development of Tillers

Bud initiation is obvious when a visible swelling occurs in the axil of a leaf primordium; however, mitotic activity on the lateral surface of the adjacent unexpanded internode foreshadows the initiation of a bud primordium long before a definite protuberance is evident.

In longitudinal section, cells in the corpus just beneath the protoderm (dermatogen) undergo periclinal divisions which give rise to a region of radially seriated cells, a stratified zone or 'shell zone' (Fig. 18). The bud initials soon become distinct from the larger corpus cells due to their more intense staining and their filar arrangement.

Continued activity in the entire sector leads to an enlargement of the tunica and corpus initials of the bud. At this stage a small protuberance is evident as a consequence of the increase in cell size and number (Fig. 19). An axillary meristem with distinguishable tunica and corpus is thus produced. At no time during the course of lateral bud initiation are periclinal divisions to be detected in the tunica.

Table 1. Organogeny of the main axis as related to time of initiation and external appearance of the plant

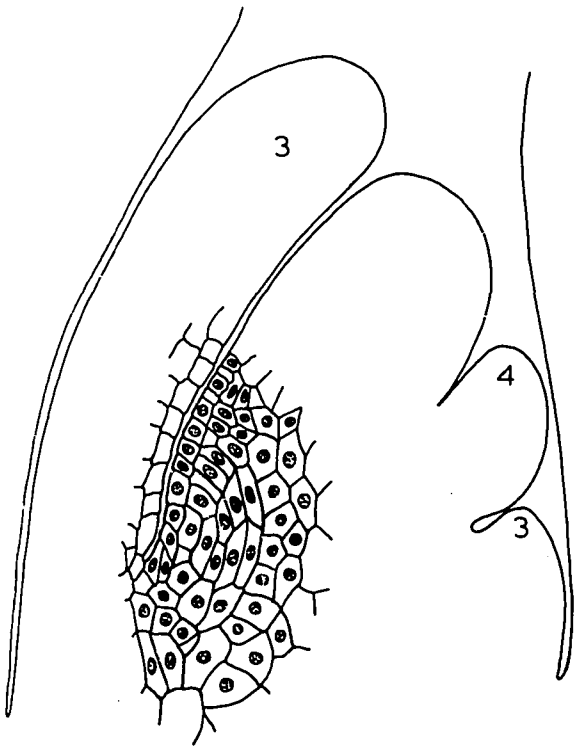
Leaf number in order of initiation	Time of initiation or occurrence, in days after imbibition has begun	External appearance of main axis of plant in field
1	--	
2	--	
3	2 (45 hours)	
4	3 1/2	
	4	Emergence from soil
5	7	Coleoptile and first foliage leaf
6	9	One or two foliage leaves
7	11	Two foliage leaves
8	12	Two or three foliage leaves
9	13	Three foliage leaves
Inflorescence branch primordia	15	Three or four foliage leaves
	17	Four foliage leaves
	21	Five foliage leaves
	27	Six foliage leaves
	33	Seven foliage leaves
	39	Eight foliage leaves
	45	Nine foliage leaves--flag leaf
	53	Emergence of panicle

Fig. 18. Stratified ("shell") zone which foreshadows the initiation of a bud in the axil of the third foliage leaf. (7 days after planting, X 320)

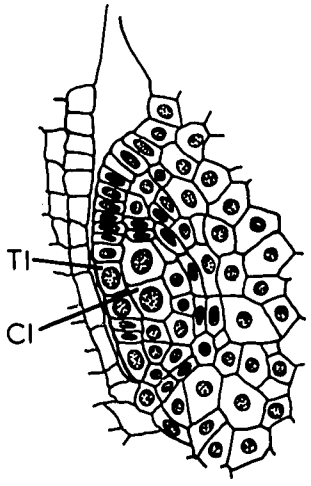
Fig. 19. Bud primordium with tunica and corpus initials. (X 320)

Tunica initials (TI)

Corpus initials (CI)



18



19

In distinct contrast, the first indication of a leaf primordium is noted by the presence of periclinal divisions in the tunica.

A stratified zone first becomes evident in the axil of the second leaf primordium from the stem apex. A definite protuberance with tunica and corpus can be observed first in the third or fourth leaf axil from the apex.

Buds on the main axis are initiated acropetally at intervals of 2 to 4 days. The term main axis is used to designate the culm that arises from the plumule. A culm that arises from an axillary bud is designated a tiller. Although the phytomer is considered the morphological unit of growth in the shoot of grasses, it is more convenient to consider an axillary bud with the leaf which subtends it. Therefore, buds 1 through 5 in Table 2 refer to lateral buds occurring, respectively, in axils of the first five foliage leaves of the main axis.

Four primary axillary buds are invariably initiated, each of which has six or seven leaves (Table 2). The primordium of a bud can occasionally be detected in the fifth leaf axil. During the examination of material for this study, there was no external indication of bud initiation in axils of foliage leaves 6 through 9 of the main axis.

Development of primary and higher orders of buds follows the same general pattern as that previously outlined for

Table 2. Development of axillary buds[a] as related to time of initiation and subsequent ontogeny

Bud		Days after planting		
On main axis	On tillers	Initiation of bud	Floral transition	Total number of leaves
C (coleoptile)		--	17	6
C' (accessory coleoptile bud)		5	--	2
1		2 1/2	17	7-8
	1			6
	2			5
	3			3
	4			0-1
2		3 1/2	17	7
	1			3
	2			2
	3			1
	4			0-1
3		5	19	6
	1			3
	2			1
	3			0-1
4		7	19	6
	1			3
	2			1
	3			1
5		11	--	0-2

[a]Axillary buds are designated by the same number as the leaf which subtends it.

the main axis. The prophyll of the lateral shoot arises on the adaxial side of the bud primordium and resembles a coleoptile in morphology and development. The prophyll is somewhat flattened on the side facing the main axis and has a longitudinal opening extending down the opposite side. The prophyll has two prominent laterally situated vascular bundles. Succeeding leaves of the bud arise with two-ranked phyllotaxy at a divergence of 90° to those on the main stem.

By the fifth day after planting a small protuberance is evident on the internode above the base of the coleoptile, just beneath the developing coleoptile bud. This represents the primordium of a second reduced or "accessory" coleoptile bud. Whereas the original coleoptile bud may have a total of six leaves, the accessory bud was observed to develop no further than the two-leaf vegetative stage (Fig. 17).

Under the field conditions of this study, one to three of the axillary buds on the main axis produced mature panicle bearing culms. The usual number was two, these arising from axillary buds 1 and 2. The main axis enters the floral transition by 15 days. By 17 days, buds in the axil of the first two foliage leaves and the larger bud in the axil of the coleoptile had undergone transition. In a count of 132 plants, only two had developed productive fruiting tillers arising from the coleoptile bud. Gross microscopic examination of all tiller buds at 40 days indicated that all apices

eventually produce at least rudimentary inflorescence primordia.

Vascular Differentiation

The procambium

Procambium strands can be detected at the level of the first or second leaf primordium below the shoot apex. The first strands are derived from the corpus of the apical meristem and are associated with leaf primordia. The procambium strand is composed of elongate prismatic cells with densely staining contents, and may be identified in transverse section when they consist of four or five cells (Fig. 23). Strands increase in diameter by longitudinal divisions until they are composed of 40 or more cells (Figs. 22, 23).

Procambium is evident in a developing leaf primordium at a distance of four or five cells from the distal margin, where the leaf is seven to nine cells in thickness (Fig. 15). In transverse aspect, a median and two lateral strands can be detected simultaneously. Each leaf primordium displays 11 to 13 procambium strands at the level of the stem apex by the time differentiation in the median strand is evident.

Procambium strands of the upper internodes of the stem are arranged in three ranks as viewed in transverse section. The two inner ranks are larger and more precocious in differentiation; bundles of the outer rank are reduced in size and

in the number of vascular elements, and are evident at a lower level in the stem (Figs. 20, 21). Differentiation of procambium will be described as it occurs in larger strands of the internodes. The pattern of procambial differentiation in other regions is essentially similar.

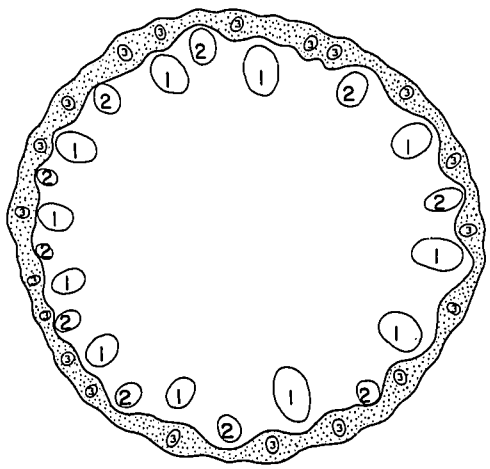
Ontogeny of the vascular bundle

The first sign of differentiation is indicated by the presence of a single protophloem sieve tube located two or three cells from the outer periphery of the strand (Figs. 22, 23). This cell has thick walls and a densely staining protoplast. Four to eight more protophloem sieve-tubes are soon differentiated centripetally. At maturity, they all appear thinner walled and lack stainable contents (Fig. 24). Subsequent growth in adjacent tissues is related to the rapid obliteration of the protophloem. This may be detected initially by the wrinkled appearance of the radial walls of the protophloem before the metaphloem is fully differentiated (Fig. 24).

The first protoxylem element is differentiated near the inner edge of the procambium strand at the end of a radial series of cells extending centripetally from the protophloem (Fig. 22). This occurs by the time two protophloem cells are mature. A total of five or six protoxylem elements are differentiated in centrifugal sequence (Fig. 24). When the last

Fig. 20. Projection drawing showing regions in the eleventh internode (peduncle). Numbers indicate first, second and third rank bundles. Stippled area indicates the hypodermal sclerenchyma. (X 40)

Fig. 21. Transverse section of eleventh internode indicating the general pattern of procambium strands. The first rank bundles have mature protophloem and some mature protoxylem, whereas the third rank (peripheral) bundles have only one or two protophloem sieve-tubes. The darkly staining subepidermal tissue indicates the region of future hypodermal sclerenchyma and chlorenchyma. (X 100)



20

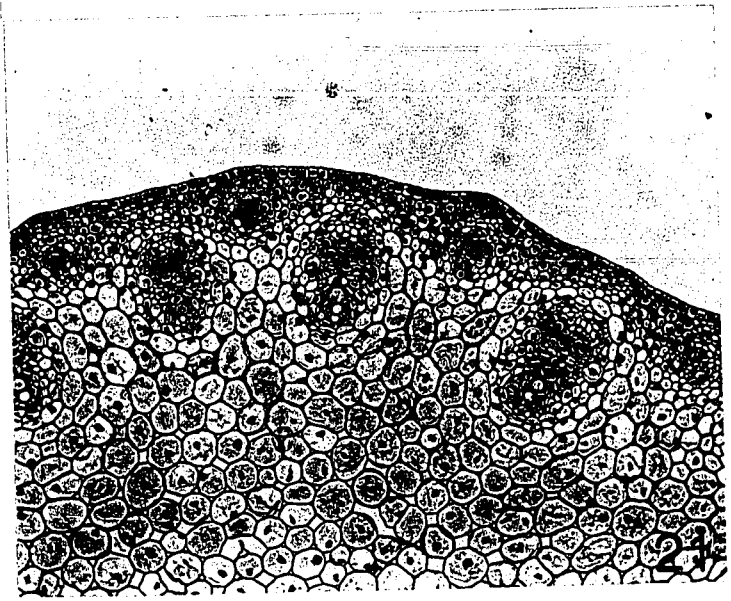


Fig. 22. Transverse section of a differentiating third rank bundle from the peduncle. A single sieve tube is evident. (49 days after planting, X 400)

Fig. 23. Procambium in the fifth leaf primordium in the first tiller bud. (19 days after planting, X 400)

Fig. 24. Transverse section of first rank bundle from the eleventh internode. The protophloem and protoxylem are immature. The cambiform zone is evident between two enlarging lateral metaxylem vessels. Both anticlinal and periclinal divisions are evident in the sheath. (49 days after planting, X 400)

Fig. 25. Transverse section of bundle of the first rank from the eleventh internode. The protophloem is obliterated and the metaphloem is almost mature. The protoxylem lacuna and two protoxylem vessels are evident. (51 days after planting, X 400)

Sieve tube	(ST)
Procambium strand	(PC)
Protophloem	(PP)
Protoxylem	(PX)
Cambiform zone	(CM)
Bundle sheath	(SH)
Obliterated protophloem	(OP)
Protoxylem lacuna	(XL)


ST
22
PC
23
PP
24
PP
25

protoxylem vessel is mature, the first three or four have been destroyed as a result of rapid internode expansion in diameter and length (Fig. 25).

By the time one or two protoxylem trachae are mature, cells near the center of the strand have undergone a series of periclinal divisions which give rise to a distinct cambiform zone. Cell divisions occur throughout the zone and produce five to seven radially seriate rows of cells (Fig. 24). Two large prominent metaxylem vessels arise at the lateral edges of the procambium strand and are first visible by the time the last two protoxylem vessels are mature. The inner derivatives of the cambiform zone develop into smaller metaxylem tracheae, located between the larger lateral vessels. A number of cells on both sides of the protoxylem remain relatively undifferentiated. This tissue is xylem parenchyma.

While the inner cells of the cambiform zone are undergoing differentiation into metaxylem elements, the outer derivatives become metaphloem 'mother cells'. Division of these cells give rise to metaphloem composed of sieve tubes and their associated companion cells. Differentiation of the metaphloem takes place centripetally. Sieve-elements are clear, except at the sieve plate, whereas companion cells are nucleate and have other stainable contents (Fig. 25). All cells in the cambiform zone eventually become differentiated, and metaphloem is then directly adjacent to mature

metaxylem (Figs. 26, 27).

The procambium cells which give rise to the bundle sheath can be detected in the early stages of bundle ontogeny as a cylinder of cells, one or two layers thick at the periphery of the strand. The cells are most conspicuous as a layer just external to the protophloem and protoxylem (Figs. 22, 23). The developing sheath increases in diameter and thickness by divisions which are both periclinal and anticlinal to the periphery of the bundle (Fig. 24). One to three layers of these cells differentiate into the sclerenchyma that encases the mature bundle (Figs. 26, 27).

Cell types in the vascular bundle

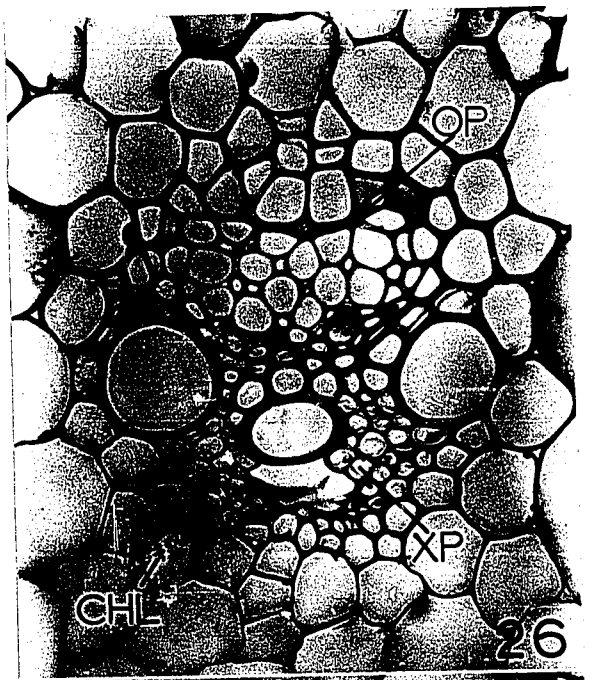
Xylem In the vascular bundles of the stem and leaf, the first two protoxylem tracheae mature very early in the ontogeny of the bundle and have annular secondary wall thickenings. These tracheae increase greatly in length and the primary walls are eventually destroyed by continued elongation (Fig. 32). The disarranged annular thickenings are evident in the lacuna in longitudinal sections.

The mature protoxylem usually consists of five vessels in radial sequence. The third and fourth elements usually have secondary wall thickening in the form of a single spiral band, or as many as three parallel bands (Fig. 33). A single vessel element may have both annular and helical thickenings.

Fig. 26. A nearly mature first rank bundle from the eleventh internode. Some metaxylem and bundle sheath cells are still nucleate. The xylem parenchyma is evident at this stage. Only one protoxylem vessel remains intact. Chloroplasts are present in some sheath cells. (57 days after planting, X 400)

Fig. 27. Transverse section of a mature vascular bundle from the seventh internode. (49 days after planting, X 400)

Obliterated protophloem	(OP)
Xylem parenchyma	(XP)
Chloroplasts	(CHL)


OP
XP
CHL
26


27

The wall thickening of the outermost protoxylem vessel is predominantly spiral, with interconnections between helices (Fig. 34). In cases where the connections between helices are numerous the vessel appears spiral-reticulate or scalariform. A single vessel cell may have annular or spiral thickenings at one level and a spiral-reticulate secondary wall at another.

The lateral secondary walls of the two large metaxylem vessels have numerous small elongate pits (Fig. 35). The pits may be less evident in areas where the vessels adjoin sheath cells or parenchyma. These vessel elements have porous ends by maturity, and a vertical column of these elements forms a continuous tracheal tube.

The smaller metaxylem tracheary elements between the two large vessels have pitting which ranges from small slits to large reticulations. The tracheary elements near the center of this zone are largely reticulate (Figs. 36, 37). Those near the periphery of the zone may have large, nearly circular pits (Figs. 28, 29). In all cases, pits on lateral walls correspond to the pits of adjacent cells. The perforation plates of these vessel members occur on the end walls. Some tracheary elements have a large single opening at each end, a simple perforation (Fig. 36), whereas others have multiple perforations. The latter may be reticulate (Fig. 37), or in the form of approximately circular holes (Fig. 38). In those

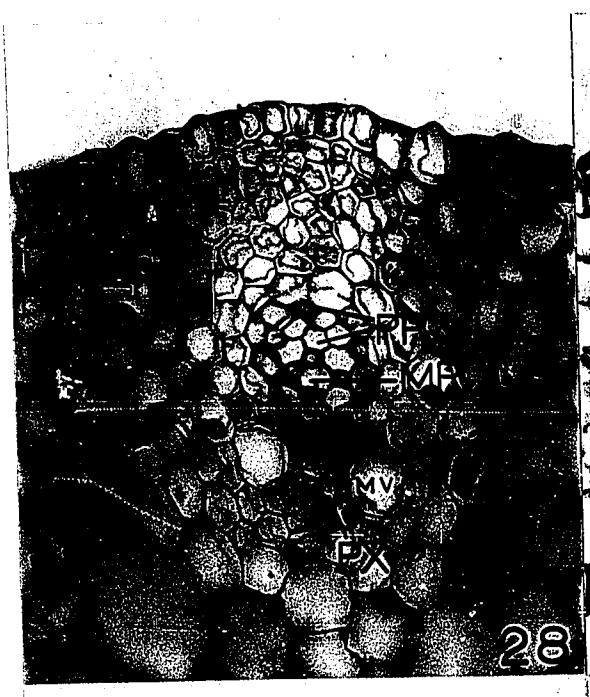
Fig. 28. Third rank bundle from the tenth internode. The protophloem and protoxylem are plainly evident, whereas protoxylem is reduced. The developing bundle sheath is more extensive at the periphery and is contiguous with the epidermis. (51 days after planting, X 400)

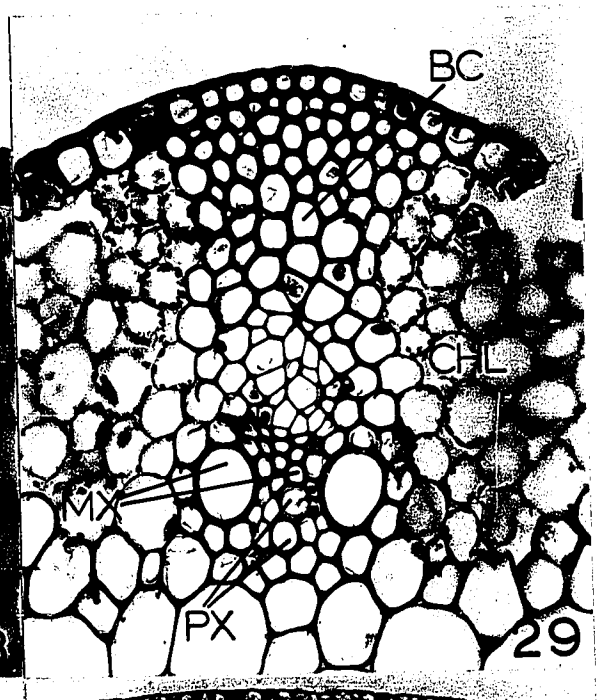
Fig. 29. A mature third rank bundle from the tenth internode. Metaphloem and metaxylem are prominent. The protoxylem is reduced to two small vessels and there is no xylem lacuna. The sheath (bundle cap) extends to the epidermis. (57 days after planting, X 400)

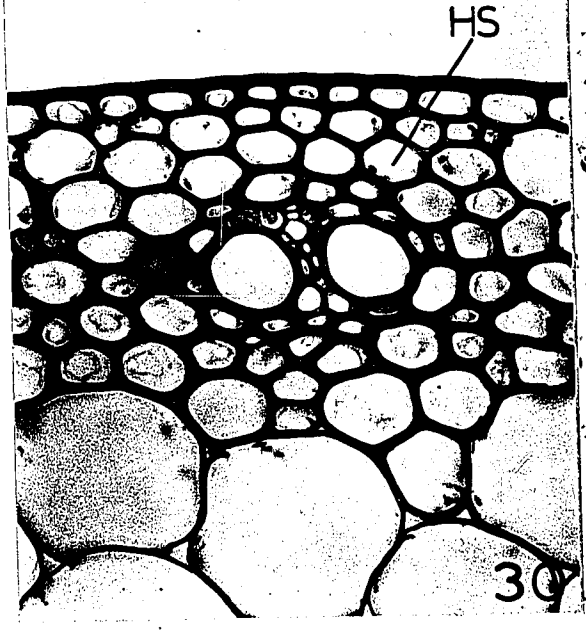
Fig. 30. A reduced third order bundle from the seventh internode. The xylem and phloem are completely surrounded by hypodermal sclerenchyma. Numerous chloroplasts are evident in the hypodermal tissue. (47 days after planting, X 400)

Fig. 31. Immature bundle at the base of a developing leaf sheath. This figure illustrates the extensive "bundle cap" which develops in basal regions of the sheath and internode. (39 days after planting, X 100)

Protophloem	(PP)
Protoxylem	(PX)
Metaxylem	(MX)
Metaphloem	(MP)
Metaxylem vessel	(MV)
Bundle cap	(BC)
Chlorenchyma	(CHL)
Hypodermal sclerenchyma	(HS)
Developing sclerenchyma	(SCL)


MV
PX
28


BC
CHL
MX
PX
29


HS
30

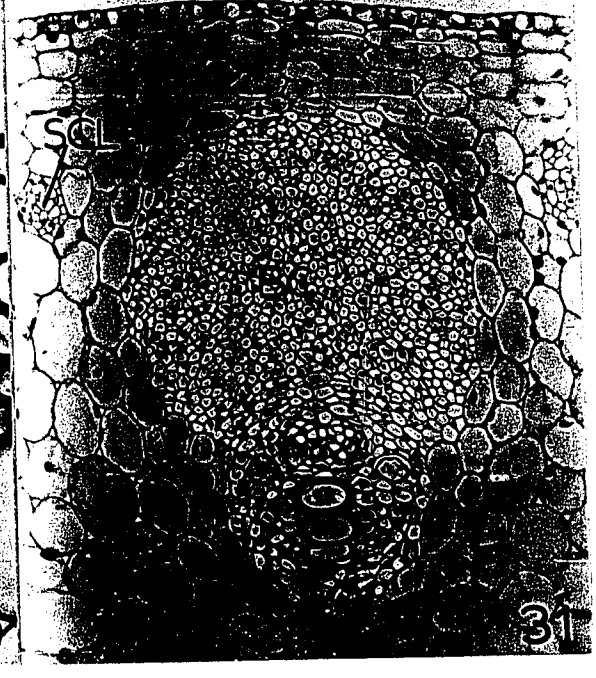

SCL
31

Fig. 32. Annular protoxylem vessel. A, unexpanded in length; B, after vessel has lengthened. (X 425)

Fig. 33. Spiral (helical) protoxylem vessel. Secondary thickening is composed of three parallel spirally coiled bands. (X 425)

Fig. 34. Spiral-reticulate protoxylem vessel. Secondary thickening is of the spiral type with cross-connecting bands. This vessel was entirely spiral at one end and more reticulate at the other. (X 425)

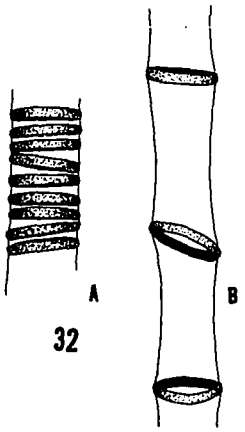
Fig. 35. Large pitted metaxylem vessel. (A, X 250; B, X 25)

Fig. 36. Reticulate metaxylem vessel with large simple perforation plate. (X 425)

Fig. 37. Reticulate metaxylem vessel with reticulate perforation plate. (A, X 425; B, X 25)

Fig. 38. Metaxylem tracheary element with tapered ends and large closely spaced circular pits. (A, X 110; B, X 425)

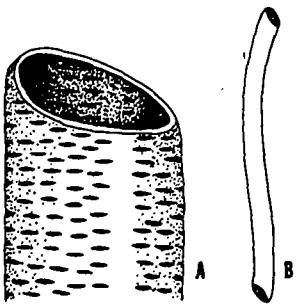
Fig. 39. Metaxylem tracheary element with tapered ends and less closely spaced circular pits. (A, X 10; B, X 425)



32

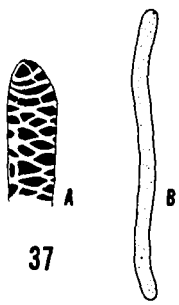
33

34

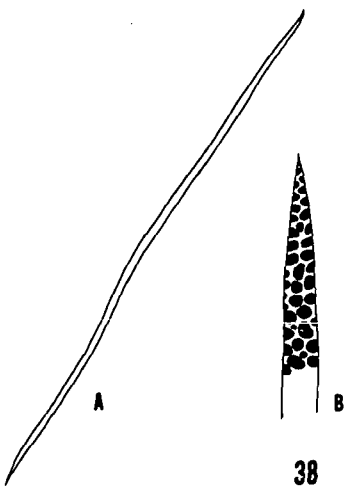


35

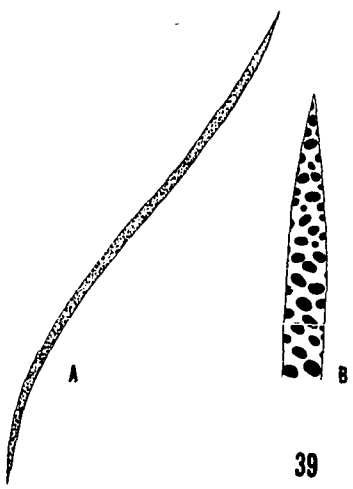
36



37



38



39

tracheary elements with tapered ends the exact area of the perforation plate is difficult to discern.

A distinctly different type of xylary element in the transitional region of the first internode contains numerous large vessels with profusely pitted secondary walls (Figs. 40, 41). Perforation plates may be present at the end or on the lateral walls, and their length is extremely variable.

Phloem The protophloem is composed of thick-walled sieve tubes which resemble those of the metaphloem. The obliterated protophloem persists in the mature bundle as a stainable substance (Fig. 27). The metaphloem sieve elements are long, enucleate cells, which have sieve plates only at the ends (Figs. 27, 42). Companion cells are shorter than adjacent sieve tubes and nucleate (Fig. 43).

Bundle sheath Cells of the bundle sheath range in structure from extremely long pitted fibers (Figs. 44, 45), to large, sparsely pitted sclerenchyma cells (Figs. 46, 47). The adjacent pith parenchyma cells have some of the characteristics of sclerenchyma. These cells become increasingly more parenchyma-like farther from the bundle (Fig. 27). Chloroplasts are present in the lignified cells of the pith which border the bundle sheath, as well as in the hypodermal sclerenchyma of the internode (Figs. 26, 27, 30).

Fig. 40. Tracheary element from the upper region of the first internode. (A, X 425; B, X 110)

Fig. 41. Tracheary element from the region of the coleoptile node. (X 425)

Fig. 42. Metaphloem sieve tube. (A, X 100; B, X 425)

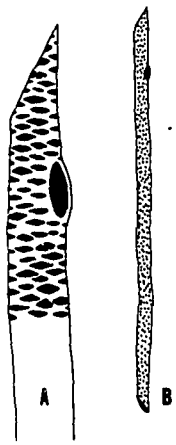
Fig. 43. Metaphloem companion cell. (A, X 425; B, X 150)

Fig. 44. Sclerenchyma fiber from bundle sheath near the zone of metaxylem. (A, X 75; B, X 425)

Fig. 45. Fiber from the hypodermal sclerenchyma. (A, X 75; B, X 425)

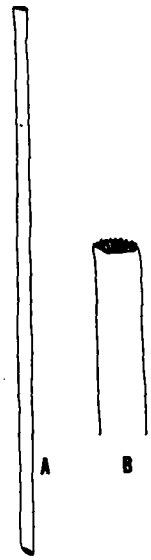
Fig. 46. Bundle sheath cell from region near metaxylem. (A, X 110; B, X 425)

Fig. 47. Bundle sheath cell. (A, X 110; B, X 425)

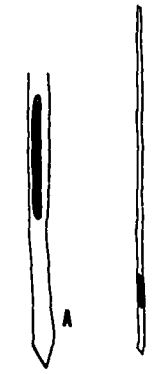


40

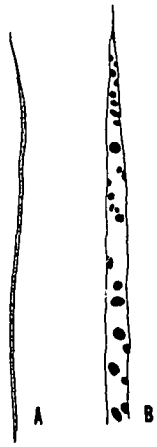
41



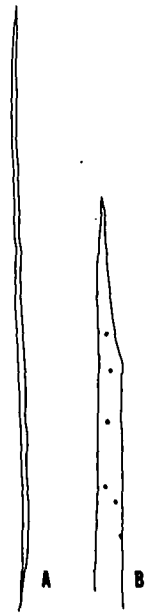
42



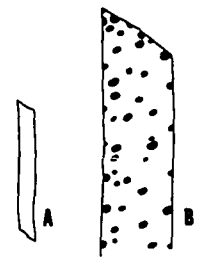
43



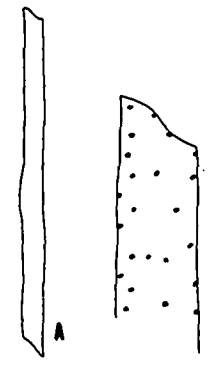
44



45



46



47

Variations in the vascular bundle

The foregoing description of vascular bundle ontogeny is based mainly on the development of the larger first and second rank bundles of the upper internodes. The peripheral, third rank bundles of the stem are reduced in size and mature later. Many of them have a pattern of development similar to that previously described for the larger bundles. The protoxylem in these bundles is disproportionately reduced and reaches maturity after the metaphloem (Figs. 28, 29).

Other peripheral bundles may be so reduced that protoxylem and protophloem appear to be entirely lacking (Fig. 30). The more reduced vascular strands are often completely surrounded by hypodermal sclerenchyma.

Vascular differentiation in the leaf blade is essentially similar to the development described for the stem. However, the vascular bundles in the intercalary zone of the sheath are strikingly different. The protoxylem is more prominent than the metaxylem, the large metaxylem vessels may be reduced or absent. The protophloem is not obliterated until the metaphloem is nearly mature. The cross-sectional area of the sclerenchyma bundle sheath external to the phloem is very large, whereas the remainder of the sheath is narrow (Fig. 31). This extensive area of mechanical tissue suggests a 'bundle cap'. Small strands of sclerenchyma are often inter-

spersed among the vascular bundles. A similar arrangement is found at the base of expanding internodes.

The coleoptile and prophyll have bundles in which the metaxylem partially surrounds the phloem. These have been referred to as 'semi-amphivasal'.

Structure of the Internodes

Variation in internodes

The first internode (mesocotyl) is transitional between the stem and root portions of the plant axis. The vascular system of this transitional region in Avena has been described by Boyd and Avery (8) as consisting of: 1) a central stele composed of two large endarch collateral bundles fused latterally with two smaller bundles, 2) a single exarch "cortical" bundle, and 3) a cortex composed entirely of thin walled parenchyma (Fig. 48).

The second, third, and fourth internodes exhibit transitional features, but more nearly resemble the upper culm. However, the individual bundles are less clearly defined, and there remains a distinct parenchymatous cortex (Fig. 49). Small vascular bundles and areas of xylem and phloem can be found in a cylinder of sclerenchyma. Amphivasal arrangement of the bundles is common. These internodes usually have a small central pith cavity.

Internodes 5, 6, 7, 8, 9, 10, and 11 compose the greater length of the culm. The peduncle is regarded here as the eleventh internode. Vascular bundles in these internodes have the distinct, three-ranked arrangement described earlier. A region of hypodermal sclerenchyma forms a continuous zone four to seven cells in thickness, just beneath the epidermis. This zone is composed of long, sparsely pitted fibers (Fig. 45). In the uppermost three or four internodes, longitudinal bands of thin-walled chlorenchyma alternate circumferentially with the hypodermis and third-rank vascular bundles (Fig. 51). Internodes below this level have chlorenchyma with thick, lignified cell walls (Fig. 50). The epidermis contains longitudinal rows of stomata adjacent to the areas of chlorenchyma. A large central pith cavity resulting from ruptured pith cells is characteristic of the upper internodes.

Relation of internode structure to lodging

The transverse aspects of internodes in two varieties of Avena were studied with regard to structural features which may be associated with resistance to lodging. Features compared in the internodes 7, 8, and 9 were: 1) culm diameter, 2) diameter of pith cavity, 3) thickness of culm wall, 4) thickness of the hypodermal sclerenchyma, 5) number of cell layers in the hypodermal sclerenchyma, and 6) number and distribution of vascular bundles.

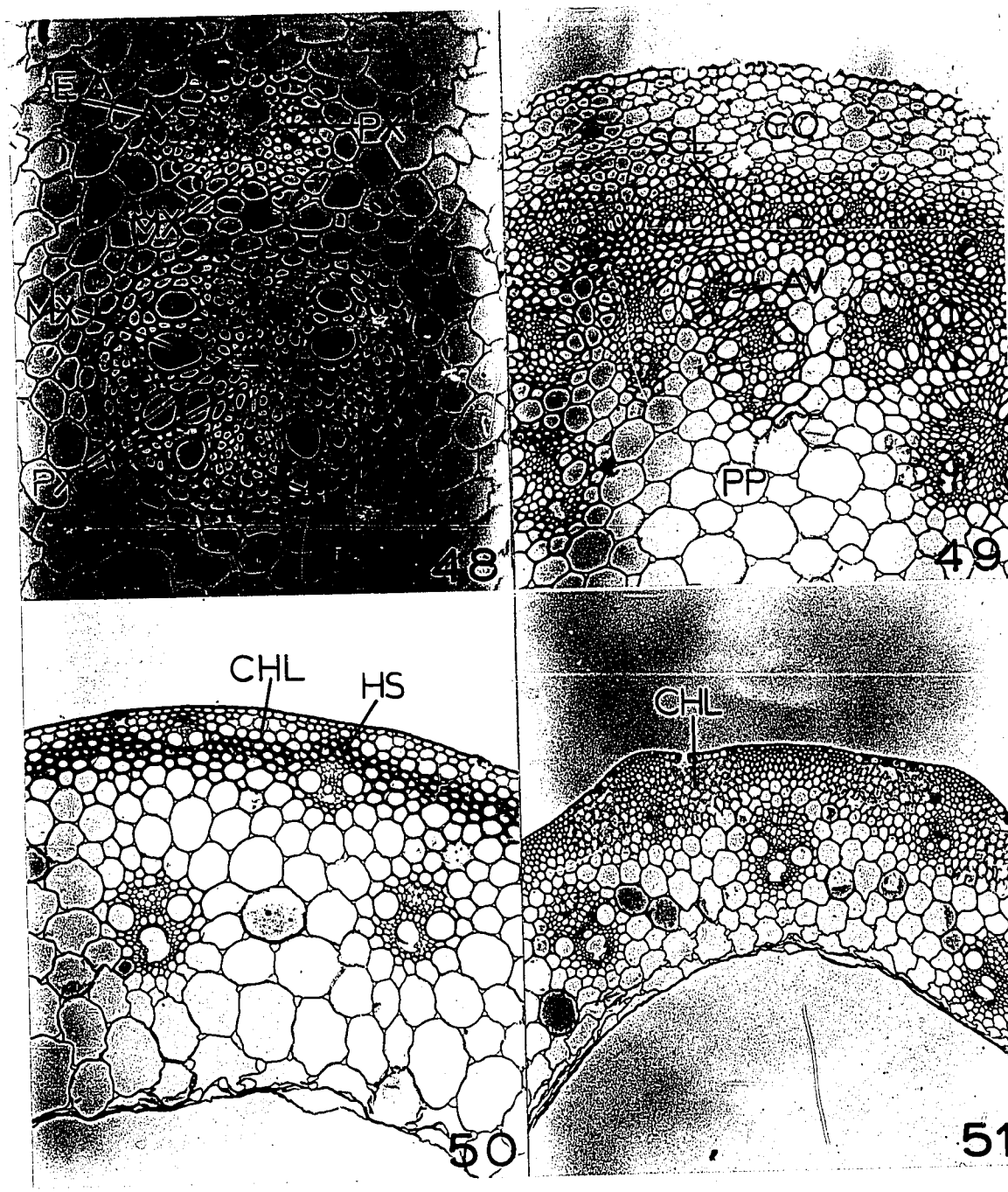
Fig. 48. Transverse section of the first internode showing a central endarch stele and an exarch vascular strand. (9 days after planting, X 150)

Fig. 49. Transection of transitional fourth internode. (47 days after planting, X 80)

Fig. 50. Transection of seventh internode. (47 days after planting, X 80)

Fig. 51. Transection of eleventh internode (peduncle). (37 days after planting, X 80)

Exarch vascular strand	(EA)
Protoxylem	(PX)
Metaxylem	(MX)
Phloem	(P)
Sclerenchyma	(SCL)
Cortex	(CO)
Amphivasal bundle	(AV)
Pith parenchyma	(PP)
Chlorenchyma	(CHL)
Hypodermal sclerenchyma	(HS)


E
PX
MX
MX
PX
48
CO
SCL
AV
PP
49
CHL
HS
50
CHL
51

The lodging resistant variety, Clintland, differed with the weak strawed variety, Marion, in having: 1) larger culm diameter, 2) greater diameter of pith cavity, 3) thicker hypodermal zone, and 4) a greater number of vascular bundles in the hypodermal zone. These differences were detected both visually and by measurements (Table 3).

The field collections upon which the foregoing data are based were made during an extremely wet season which led to exceptionally tall and luxuriant growth. The amount of culm

Table 3. Some anatomical features of the seventh internode of the main axis as they are related to two varieties which differ in lodging resistance[a]

	Clintland		Marion	
	Mean[b]	Range	Mean	Range
Culm diameter, mm.	4.60	.25	4.15	.25
Diameter of pith cavity, mm.	3.08	.42	2.64	.40
Thickness of culm wall, mm.	.76	.19	.76	.11
Thickness of hypodermis, mm.	.09	.03	.07	.02
Total number of vascular bundles	52	6	49	7
Vascular bundles in hypodermis	20	5	15	4
Cell layers in hypodermis	4	0	4	0

[a]Clintland has strong straw and Marion has weak straw, as classified by Norden (25).

[b]Sample number: Clintland = 9, Marion = 7.

breakage was negligible; but lodging at ground level was severe. Lodging, in this case, appeared to be related to root anchorage rather than stem strength.

DISCUSSION

The more recent studies of the homologies of the embryo in the grasses appear to substantiate Avery's (5) interpretation of the anatomy of the Avena embryo. Homology between the coleoptile and prophyll, as the first plumular leaf and the first leaf of an axillary bud, respectively, is suggested by their developmental similarities. They each have two lateral vascular bundles with semi-amphivasal arrangement. There is a similar pattern of eventual destruction in these two structures in which a large schizogenous cavity develops in the parenchyma between the inner and outer epidermal layers.

The apical meristem of the post dormant embryo and young seedling has a distinct tunica-corpus organization. Divisions in the single-layered tunica are anticlinal except at the point where a new leaf primordium is initiated. Cells of the corpus divide in random planes. During the initiation of the last three or four foliage leaves the outer cells of the corpus appear to be periclinally stratified. Sharman (32) has identified four zones in the apex of Agropyron repens: dermatogen, hypodermis, subhypodermis, and central core. Hamilton (20) extended this interpretation to Avena. Kliem (22) interpreted these zones in the Avena shoot apex as stratification of the corpus. Although divisions in the sub-tunica layers are predominantly anticlinal, periclinal divisions are occasionally found prior to floral transition. The doubtful

autonomy of such layers and their absence in the early stages suggests a preference for the designation of the apical meristem as a corpus enclosed by a one or two layered tunica. This would be compatible with the occurance of a two-layered tunica during organogeny as reported by Holt (21).

The apical meristem of the shoot in Avena contains a zone of three to five large corpus cells at the tip. Cells of the tunica adjacent to this region are also larger. Immediately proximal to this zone are linear files of cells which are derivatives of the former.

The same pattern of apical initials is established early in the ontogeny of axillary buds. Two or three large corpus initials and two or three large tunica initials are evident by the time a small bud protuberance is initiated. This organization lends evidence in favor of the concept of an apical meristem being composed of a small zone of initials and their derivatives, rather than clear-cut, permanently defined layers and their derivatives.

A general increase in the size of the apical meristem is evident during successive plastochrons of the Avena shoot apex: the increase in volume results from an increase in cell number. Hamilton (20) reported a slight decrease in cell size of the meristem of Avena during later stages. Occurring with the general increase in size of the apical meristem is a rapid lengthening of the stem tip and an asso-

ciated shortening in the duration of successive plastochrons.

Sharman (33) speculated that in Agropyron the marginal meristem of a leaf primordium is concerned with the formation of the bud which will later appear in the axil of the leaf below. This interpretation does not appear applicable in Avena, since divisions foreshadowing the initiation of a bud are present before the leaf meristem completely surrounds the stem. Furthermore, the initial periclinal divisions associated with bud formation are relatively deep within the corpus, whereas those associated with the leaf are relatively superficial.

The total number of foliage leaves has previously been reported in oats to vary from six to eight (20, 21). However, in the varieties used in the present studies on Avena the number of foliage leaves was invariably nine. This was determined by numerous careful dissections throughout the growing season and by examination of serial paraffin sections of the shoot apex at different stages of development. The question of whether leaf number is a constant feature of a variety or whether it is environmentally controlled should be studied further.

The vascular ontogeny described here for Avena is essentially similar to that reported for maize by Esau (10) and Sharman (31).

Although Cheadle (9) has suggested that all xylary

elements in Avena are vessels, the structure and extent of perforation plates should be investigated further. If definite perforation plates are absent in some of the tracheary elements with tapered ends, they would properly be classified as tracheids.

Distinct differences in xylary elements can be observed when they are studied with regard to their time of origin and structure. Goodwin (18) found a close correlation between cessation of elongation of the first internode and the development of pitted vascular elements. He suggests further study on the possible role of pitted, non-elastic xylem elements in limiting elongation. Regardless of whether metaxylem functions mechanically in limiting elongation, protoxylem is associated with elongating phase and metaxylem is associated with nonelongating phase of structures. The third rank (peripheral) vascular bundles have very little protoxylem and they differentiate after elongation of the stem has ceased. Conversely, at the base of leaf sheaths and stem internodes where the elongation phase is extended over a longer period of time, the metaxylem of the vascular bundles is poorly developed and the protoxylem is well developed.

The sparsely pitted sclerenchyma cells which form the sheaths of the internodal bundle vary in length. Those with a small transverse diameter tend to be long and fiber-like with tapered end walls. On the other hand, the larger sheath

cells are short, the length sometimes being not more than five times the transverse diameter. The sheath is often indistinct from the interfascicular tissue which may be as heavily lignified as the sheath cells. This has also been noted in maize, Esau (10), Sass (29), Magee (23). However, the sclerified pith is composed of short, sometimes almost isodiametric cells, and has conspicuous intercellular spaces. These characteristics indicate the cells are basically parenchyma with more or less lignified secondary walls.

The massive "bundle cap" found in the basal regions of the leaf and the internodes has been described in sugar cane, Artschwager (4), and maize, Esau (10), as being collenchyma. However, it is questionable whether such an interpretation is applicable to Avena. The cells are long and fiberlike, there is an absence of intercellular spaces, and the lignified secondary wall is uniformly thickened in transverse and longitudinal aspects. Furthermore, collenchyma is not typically related by position or derivation to vascular bundles. It is therefore suggested that this tissue in Avena be referred to as sclerenchyma.

Although a total of more than 20 axillary buds were often detected on a single oat plant, there were rarely more than two buds which developed into fruiting tillers in the plantings studied. It was also found that all buds eventually undergo floral transition and develop inflorescence primordia.

It is thus evident that the potential number of fruiting culms is quite large. Frey and Wiggins (15, 16) have shown that the environment and agronomic practices can influence the number of emerged fruiting tillers produced by a plant. It may therefore be possible to increase significantly the number of productive culms by appropriate treatment.

SUMMARY AND CONCLUSIONS

A study was made of the developmental vegetative morphology of Avena sativa L., with emphasis on reactivation and resumption of growth in the dormant embryo, initiation and development of leaves and axillary buds, vascular ontogeny, and structure of the internodes.

The plumule in the dormant Avena embryo contains two foliage leaf primordia enclosed by the coleoptile. There are two seminal roots in addition to the radicle. Vascularization in the dormant embryo is represented by partially differentiated procambium strands.

Twelve hours after imbibition, the radicle has penetrated the pericarp. Postdormant growth of the coleorhiza, epiblast, and scutellum is by cell enlargement only.

Mitotic divisions occur by 24 hours, and are first evident in the radicle, and by 27 hours figures are abundant in the radicle, seminal roots, coleoptile node, and first foliage leaf. Complete mitotic reactivation takes place by 36 hours, and division figures are then most abundant in the stem and root apices, and in the leaf primordia.

The apical meristem of the oat seedling has a distinct tunica and corpus. Each leaf is initiated by a periclinal division in the tunica. An annular leaf primordium is established by the peripheral spread of these divisions around the

apex. Both the tunica and the corpus contribute to the leaf primordium, after the initiating divisions in the tunica.

The first post-dormant leaf, which is the third foliage leaf, is initiated within 45 hours. The interval between successive plastochrons varies from 1 to 3 days. Nine foliage leaves are initiated, followed by transition to the floral phase as early as 10 days after emergence from the soil.

Procambium strands are first evident at the level of the first or second leaf primordium below the apex, where they consist of four or five cells in transverse aspect. Strands increase in diameter until they consist of 40 or more cells. Radially mid-way in the strand, cell divisions presently become predominantly tangential, and produce a transverse cambiform zone of derivatives.

Protophloem becomes evident first on the side of the procambium toward the outside of the stem, or the dorsal side of the leaf. The protophloem consists only of sieve tubes. The first protoxylem element is differentiated after two or three protophloem cells mature, on the side of the strand opposite the protophloem. The protoxylem consists of annular, spiral, and spiral-reticulate vessels, differentiated radially in that order. The protophloem and protoxylem are destroyed during the differentiation of the metaphloem and metaxylem.

The metaphloem consists of sieve tubes and companion

cells. The metaxylem is composed of two large vessels with small slit-like pits, and numerous tracheary elements with circular or reticulate pitting. The latter have simple or reticulate perforation plates.

The bundle sheath is derived from peripheral cells of the procambium and at maturity is not sharply delimited from the adjacent interfascicular tissue.

Axillary bud initiation is foreshadowed by periclinal divisions in the corpus in the axil of the second leaf below the stem apex. The resulting stratified zone gives rise to the corpus initials of the bud. The tunica of the bud is derived from the protoderm of the main axis.

Buds are initiated acropetally in the axils of the first four or five foliage leaves at intervals of 2 to 4 days. An accessary bud, in addition to the one present in the dormant embryo develops in the axil of the coleoptile. All axillary (tiller) buds undergo floral transition after the transition of the main axis. The tiller buds in the first and second foliage leaves usually develop into fruiting culms.

The first internode (mesocotyl) is transitional between the stem and root. Internodes 2, 3, and 4 also exhibit transitional features, but more nearly resemble the higher internodes. Internodes 5 through 11 are nearly alike histologically and compose the greater length of the culm.

Lodging resistance in oat stems is associated with:

1) larger culm diameter, 2) greater diameter of pith cavity, 3) thicker hypodermis, and 4) greater number of vascular bundles in the hypodermis. However, in the varieties studied it is suggested that the root system may be a greater factor in lodging than is the mechanical strength or tissue organization of the stem.

LITERATURE CITED

1. Abbe, E. C. and B. O. Phinney. The growth of the shoot apex in maize: external features. Amer. Jour. Bot. 38: 737-744. 1951.

2. _____, B. O. Phinney, and D. E. Baer. The growth of the shoot apex in maize: internal features. Amer. Jour. Bot. 38: 744-751. 1951.

3. _____, L. F. Randolph, and J. Einset. The developmental relationship between shoot apex and growth pattern of leaf blade in diploid maize. Amer. Jour. Bot. 28: 778-784. 1941.

4. Artschwager, E. Anatomy of the vegetative organs of sugar cane. Jour. Agr. Res. 20: 197-221. 1925.

5. Avery, B. S. Jr. Comparative anatomy and morphology of embryos and seedlings of maize, oats, and wheat. Bot. Gaz. 89: 1-39. 1930.

6. _____ and P. R. Burkholder. Polarized growth and cell studies on the Avena coleoptile, phytohormone test object. Bul. Torr. Bot. Club. 63: 1-15. 1936.

7. Barnard, C. Floral histogenesis in the monocotyledons. Aust. Jour. Bot. 5: 1-20. 1957.

8. Boyd, Lucy and G. S. Avery, Jr. Grass seedling anatomy: the first internode of Avena and Triticum. Bot. Gaz. 97: 765-779. 1936.

9. Cheadle, V. I. The occurrence and types of vessels in the various organs of plants in the Monocotyledoneae. Amer. Jour. Bot. 29: 441-450. 1942.

10. Esau, K. Ontogeny of the vascular bundle in Zea Mays. Hilgardia. 15: 327-368. 1943.

11. _____. Origin and development of the primary vascular tissues in seed plants. Bot. Rev. 9: 125-206. 1943.

12. Evans, M. W. and F. O. Grover. The developmental morphology of growing point of the shoot and the inflorescence in grasses. Jour. Agr. Res. 61: 481-521. 1940.

13. Foster, A. S. Comparative studies on the structure of the shoot apex in seed plants. Bul. Torr. Bot. Club. 68: 339-350. 1941.

14. _____. Problems of structure, growth, and evolution in the shoot apex of seed plants. Bot. Rev. 5: 454-470. 1939.

15. Frey, K. J. and S. C. Wiggans. Tillering studies in oats: I. Tillering characteristics of oat varieties. Agr. Jour. 49: 48-50. 1957.

16. _____ and _____. Tillering studies on oats: IV. Effect of rate and date of nitrogen fertilizer application. Iowa Acad. of Sci. 64: 160-167. 1957.

17. Gifford, E. M. The shoot apex in angiosperms. Bot. Rev. 20: 477-529. 1954.

18. Goodwin, R. H. On the development of xylary elements in the first internode of Avena in dark and light. Amer. Jour. Bot. 29: 818-828. 1942.

19. Hamilton, D. G. Certain oat culm characters and their relationship to lodging. Scien. Ag. 21: 646-675. 1940.

20. Hamilton, H. H. A developmental study of the apical meristem in four varieties of Avena sativa grown at two constant temperatures. Amer. Jour. Bot. 35: 656-665. 1948.

21. Holt, I. V. Cytohistological responses of varieties of Avena to 2,4-D. Iowa State College Jour. Sci. 29: 581-629. 1955.

22. Kliem, F. Vegetationspunkt and blattanlage bei Avena sativa. Beitr. Biol. Pfl. 24: 281-310. 1937.

23. Magee, J. A. Histological structure of the stem of Zea Mays in relation to stiffness of stalk. Iowa State College Jour. Sci. 22: 257-268. 1948.

24. McCall, M. A. Developmental anatomy and homologies in wheat. Jour. Agr. Res. 28: 283-321. 1934.

25. Norden, A. J. Factors associated with lodging resistance in oats. Unpublished Ph. D. Thesis. Ames, Iowa, Iowa State College Library. 1958.

26. Picklum, W. E. Histological and cytological changes in the maize embryo during germination. Unpublished Ph. D. Thesis. Ames, Iowa, Iowa State College Library. 1953.

27. Reeder, J. R. The embryo of Streptochaeta and its bearing on the homology of the coleoptile. Amer. Jour. Bot. 40: 77-80. 1953.

28. Rösler, P. Histologisch studien am vegetationspunkt von Triticum vulgare. Planta. 5: 28-29. 1928.

29. Sass, J. E. Vegetative morphology. In Sprague, G. F., ed. Corn and corn improvement. pp. 63-87. New York, N.Y., Academic Press, Inc. 1955.

30. Sharman, B. C. The biology and developmental morphology of the shoot apex in the Gramineae. New Phytologist. 46: 20-34. 1947.

31. _____. Developmental anatomy of the shoot of Zea Mays L. Ann. Bot. n.s. 6: 245-282. 1942.

32. _____. Leaf and bud initiation in the Gramineae. Bot. Gaz. 106: 269-289. 1945.

33. _____. Shoot apex in grasses and cereals. Nature, London. 149: 82. 1942.

34. Toole, E. H. The transformations and course of development of germinating maize. Amer. Jour. Bot. 11: 325-350. 1924.

35. Tucker, S. C. Ontogeny of the etiolated seedling mesocotyl of Zea Mays. Bot. Gaz. 118: 160-174. 1957.

36. Welton, F. A. and V. H. Morris. Lodging in oats and wheat. Ohio Agr. Expt. Sta. Bul. 471. 1931.

37. Yung, Chi-Tung. Developmental anatomy of the seedling of the rice plant. Bot. Gaz. 99: 786-802. 1938.

ACKNOWLEDGEMENTS

The author wishes to express his sincere appreciation to Dr. John E. Sass who suggested this study and who gave invaluable direction and assistance during the entire course of the investigation. Appreciation is due Dr. K. J. Frey for provision of the field plots and seed used in this study. Gratitude is also extended to the Quaker Oats Company which sponsored a research assistantship for the writer during a portion of these investigations.